

# How to predict plant functional types using imaging spectroscopy: linking vegetation community traits, plant functional types and spectral response

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## Summary

1. The comparable and integrated nature of plant functional types and advances in high-spectral-resolution remote sensing techniques (i.e. imaging spectroscopy) make their combination highly interesting for spatially continuous and repeatable large-scale ecosystem monitoring. Depending on physical environment and stress, plants invest in covarying biochemical and structural traits, influencing spectral characteristics of vegetation. These traits are assumed to bear a more direct causal relationship to plant functional types than to plant life/growth forms. However, the connection between a vegetation community's functional and spectral response remains to be established.

2. We assessed the correlation structure between (i) biochemical and structural vegetation traits (biomass, dry matter content, nitrogen content, neutral detergent fibre content), (ii) plant life/growth forms and (iii) seven plant functional types of two categories (strategy types, indicator values) collected in heterogeneous alpine grassland. We then used airborne imaging spectroscopy data from the same area to model and predict plant life/growth forms and plant functional types at the vegetation community level using partial least squares regression and validated our models based on an independent data set.

3. We found high correlations between many of the biochemical and structural vegetation traits, plant life/growth forms and plant functional types tested. Using airborne imaging spectroscopy data, we successfully modelled and predicted most plant life/growth forms ( $R^2$  max. = 0.56) and all plant functional types ( $R^2$  max. = 0.62). However, model performance for plant life/growth forms decreased substantially during external validation and overall model consistency was low (average change in  $R^2$  = 72%), while plant functional type models were much more consistent (average change in  $R^2$  = 20%). Based on our findings, we developed a conceptual framework using the theory and methodology of vegetation ecology and imaging spectroscopy to link the vegetation community's functional to its spectral signature.

4. Our results encourage the use of plant functional types in imaging spectroscopy in order to aid the large-scale monitoring of ecosystems, which is particularly important given the increased availability of airborne data and the prospective launches of spaceborne instruments in the near future.

**Key-words:** alpine grassland, CSR strategy type, growth form, indicator value, life form, partial least squares regression

## Introduction

To mitigate the effects of rapid global change, methods enabling timely, frequent, comparative and large-scale monitoring of vegetational properties indicative of ecosystem function are becoming increasingly important (Pettorelli *et al.* 2016). Remote sensing provides the only realistic means to

acquire spatially continuous environmental data at high spatial and temporal resolution, from which necessary consistent monitoring schemes may be developed. However, until recently remote sensing applications focused on simple land cover classifications based on plant life forms and growth forms (Schimel, Asner & Moorcroft 2013), and less on functional characteristics of vegetation communities.

Plant life and growth forms mirror different adaptations to environmental conditions based on morphological traits (e.g. Mueller-Dombois & Ellenberg 1974). They are not only used

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to map the world's major biomes (e.g. Prentice *et al.* 1992), but also serve frequently as input for ecosystem modelling (e.g. in dynamic global vegetation models; Sitch *et al.* 2003; Krinner *et al.* 2005). Recently, the widespread use of plant life and growth forms for ecosystem modelling was criticized (Van Bodegom *et al.* 2012; Yang *et al.* 2015), because plant functional traits are highly variable within life/growth forms and overlap broadly among them (Reich, Walters & Ellsworth 1997; Wright *et al.* 2004; Kattge *et al.* 2011). Alternatively, using plant functional traits directly as modelling input was suggested (Van Bodegom *et al.* 2012; Yang *et al.* 2015; Jetz *et al.* 2016), because the relationships between a variety of plant functional traits (e.g. carbon : nitrogen (C : N) ratios, specific leaf area, photosynthetic capacity, osmotic potential) and ecosystem functions (e.g. climate and water regulation, carbon storage, disturbance tolerance) are well-established (Cornelissen *et al.* 2003; Kattge *et al.* 2011). However, field measurements of plant functional traits, which are essential for model validation, are costly, time-consuming and notoriously difficult to acquire, especially in remote areas. In contrast, plant functional types can be deduced from botanical inventories (relevé data), which are more widely available than plant functional trait measurements (Reich, Wright & Lusk 2007). Most importantly, plant functional types are causally linked to biochemical, structural, physiological or demographic plant functional traits, which have been shown to follow global patterns (Reich, Walters & Ellsworth 1997; Cornelissen *et al.* 2003; Wright *et al.* 2004; Reich, Wright & Lusk 2007). While species composition of vegetation communities varies both among and within biomes, the roles and functions of plants within ecosystems are comparable (Lavorel *et al.* 1997; Tilman *et al.* 1997). These roles and functions represent different strategy types, which are combinations of covarying functional traits (Zonneveld 1983; Grime *et al.* 1997), and form the basis for plant functional type classifications (Lavorel *et al.* 1997; Tilman *et al.* 1997). Plant functional types group species having similar ecological amplitudes and responses to environmental conditions (Box 1996; Seménova & van der Maarel 2000), making them useful for bioindication, prediction of ecosystem resistance to and resilience after disturbance, and for modelling global change scenarios (Lavorel *et al.* 1997; Tilman *et al.* 1997; Díaz & Cabido 2001; Poulter *et al.* 2011).

The CSR plant strategy type system (Grime 1974, 1977), for example, categorizes plants according to their abilities to compete for resources (C strategists), tolerate stress (S strategists) and survive disturbance (R strategists), recognizing the interplay of plant functional types, plant functional traits and ecosystem functions. C strategists often dominate in low-stress (sufficient nutrients, water, light) and low-disturbance (little damage to plant material) environments, where they considerably invest in photosynthesis and fast growth (Grime *et al.* 1997; Hodgson *et al.* 1999). S strategists are, in contrast, indicative of low-disturbance, high-stress environments, where they grow slowly and flower late and briefly, but live long. R strategists, in turn, are predominantly found in environments having high disturbance frequencies, where they grow fast and flower early, but are short-lived (Grime 1977; Cerabolini *et al.*

2010). Tight correlations between CSR strategy types and a range of plant functional traits representing the world-wide leaf economics spectrum (e.g. leaf mass per area, leaf N content, leaf life span; see Wright *et al.* 2004) were confirmed across a variety of ecosystems (Hodgson *et al.* 1999; Cerabolini *et al.* 2010; Negreiros *et al.* 2014). These results strongly suggest that the CSR strategy type system should prove useful for bioindication, ecosystem monitoring and ecological modelling on a global scale. Similar to CSR strategy types, Ellenberg's indicator values for species (Ellenberg *et al.* 1991) are tightly linked to plant functional traits indicative of ecosystem functioning. This is because the system was built around species showing unimodal, monotonically increasing or decreasing responses to environmental conditions (e.g. soil moisture, soil nutrient availability, light availability), and relatively narrow amplitudes around their optima (ter Braak & Looman 1986). Although originally developed for bioindication in central Europe (Ellenberg *et al.* 1991), indicator values have been successfully applied in a variety of ecosystems, as species can be added and their values adjusted (see Diekmann 2003 and references therein).

Remote sensing applications for ecosystem monitoring could benefit from the causal relationships between plant functional traits and plant functional types; however, the link between the vegetation community's spectral (Asner & Martin 2008) and functional signatures (Hunt *et al.* 2004) remains to be established. Generally, the spectral response of vegetation is determined by reflection, transmission and absorption of light, which is caused by the structure and chemical characteristics of plant tissues, and the three-dimensional structure of the canopy. Imaging spectroscopy captures the spectral response in many narrow, spectrally contiguous bands (Schaeppman 2007), and has enabled the prediction of a series of biochemical and structural vegetation traits at the community level (Kokaly *et al.* 2009; Homolová *et al.* 2013; Asner *et al.* 2014; Schaeppman *et al.* 2015). While certain regions of the spectrum are known to be sensitive to biochemical or structural traits (e.g. Curran 1989), other plant characteristics involve several, partly overlapping spectral features (Kokaly *et al.* 2009). Detecting complex chemical and structural characteristics in an over-determined spectral signal was a common problem in chemometrics (Martens 2001), which can be solved using pattern detection techniques, such as partial least squares regression (PLSR; Wold, Martens & Wold 1983). As the independent effects of biochemical and structural vegetation traits are assumed to be largely preserved in the overall shape of the spectral response (Kokaly *et al.* 2009), pattern detection techniques can be applied to imaging spectroscopy data to search for the combined spectral features which describe, for example, plant functional types.

Given the causal relationships between biochemical and structural vegetation traits and plant functional types, we deduce that the spectral signature of plant functional types is preserved in the vegetation community's spectral response. Further, we infer that PLSR coefficients can serve as proxies for the combined biochemical and structural characteristics of plant functional types, as they are represented in the

vegetation's spectral response. This should allow us to predict plant functional types at the community level using imaging spectroscopy. In addition, we hypothesize that plant functional types can be predicted more consistently compared to plant life/growth forms. To test our hypotheses, we (i) investigated the conceptual basis for linking plant life/growth forms and plant functional types to the vegetation's spectral response by assessing their correlation to a series of vegetation traits, that is biomass, dry matter (DM), N and neutral detergent fibre (NDF) content, (ii) used airborne imaging spectroscopy data to model and predict plant life/growth forms and plant functional types using PLSR and (iii) tested model consistency using an independent data set.

## Materials and methods

### STUDY AREA

Our study area, the Swiss National Park (SNP), is located in south-eastern Switzerland (46°37' N, 10°5' E). Elevation ranges from 1350 to 3170 m a.s.l., average annual precipitation is  $754 \pm 164$  mm (mean  $\pm$  SD) and average annual temperature is  $0.9 \pm 0.5$  °C, having average annual minima of  $-29.1 \pm 2.7$  °C and average annual maxima of  $24.5 \pm 1.0$  °C (recorded between 2004 and 2013 at 1968 m). About 86 km<sup>2</sup> of the SNP's total area (172 km<sup>2</sup>) is covered by vegetation, wherein forests occupy 53 km<sup>2</sup> and grasslands 29 km<sup>2</sup>. The growing season lasts from mid-May until mid-September. The SNP was founded in 1914 and is classified as an IUCN (International Union for the Conservation of Nature) category 1a strict nature reserve. Despite over 100 years of strict protection and absence of management, the influences of former land use practices, mostly herding of cattle and sheep, haying, but also past irrigation systems, can still be seen in today's vegetation communities (Schütz *et al.* 2003, 2006). The land use history, as well as microrelief variability and grazing patterns of herbivores (e.g. Risch *et al.* 2015) influence plant  $\alpha$ - and  $\beta$ -diversity levels in our study area, with the number of plant species ranging from <10 to over 50 per 1 m<sup>2</sup>.

### BOTANICAL DATA

We collected community-level trait and relevé data in 50 research plots measuring 6 × 6 m in the SNP's grasslands. The plots covered a wide range of expositions, altitudes, vegetation productivity and community composition, but were placed in areas homogeneous in plant species composition and cover (for details, see Schweiger *et al.* 2015). To assess biochemical and structural vegetation traits, we clipped 1 m<sup>2</sup> of vegetation on the day of the imaging spectrometer overflight in the centre of each plot. We immediately sealed the samples into plastic bags, determined fresh (g m<sup>-2</sup>) and oven-dry biomass (g m<sup>-2</sup>; dried at 65 °C for 48 h) and calculated DM content (mg g<sup>-1</sup>; DM = oven-dry biomass/fresh biomass). Nitrogen and NDF contents (in %) of 24 of the 50 samples were chemically analysed using standard laboratory methods (TruSpec CN Analyzer, Leco Corp., St Joseph, MI, USA; Fiber Analyzer 200, Ankom Technology, Macedon, NY, USA). These samples were used to recalibrate our laboratory near-infrared reflectance spectrometer models (NIR Multi-Purpose Analyser; Bruker Optics, Fällanden, CH, Switzerland), generated from more than 300 vegetation samples collected within the SNP's grasslands in previous

years. Nitrogen and NDF contents of all 50 samples collected were then predicted based on near-infrared reflectance spectroscopy, having precisions of  $R^2 = 0.93$  for N and  $R^2 = 0.81$  for NDF content. Community-level traits in the research plot data set ranged between 4.7 and 2281 g m<sup>-2</sup> for biomass, 18.3% and 53.3% for DM content, 1.1% and 4.0% for N content, and 37.7% and 67.6% for NDF content. For relevé data collection, we estimated plant species cover (in %) for all species occurring in 1 × 1 m quadrats randomly placed within the 50 research plots, but avoiding previously clipped areas. In total, 170 plant species were recorded in the research plots, ranging from 6 to 41 species per plot.

An independent relevé data set (hereafter referred to as external validation data) was obtained from the SNP's long-term permanent grassland monitoring project. Briefly, 160 permanent plots of variable size and distributed over the entire area of the SNP were established as early as 1917 and are visited every 5 to 10 years and plant species cover (in %) is recorded. We selected data collected between 2006 and 2014, resulting in a data set comprising 36 plots, measuring between 1 and 320 m<sup>2</sup> in size and distributed over the entire SNP. Again, the plots covered a wide range of exposition, altitude, productivity and vegetation communities. In total, 224 species were recorded in the external validation data set, ranging from 4 to 81 species per plot.

For allocating life and growth forms, we classified each plant species as graminoid, forb, legume or shrub (life form), subdivided the graminoids into tussock and stolon plants (growth form) according to their dominant habitus in the SNP's grasslands and summed their cover % in each plot. We used Landolt & Bäumler (2010) for allocating CSR strategy types and indicator values for soil nutrients, soil moisture, light availability and mowing tolerance, which list ecological characteristics of 5500 central European plant species. We standardized the research plot and external validation data sets to 100% cover per plot and multiplied both plots × species matrices with the CSR strategy type scores and indicator values matrices, respectively (see Wildi 2010). Species classified as indifferent or with missing CSR scores or indicator values were omitted.

We included life/growth forms in our study in order to have a baseline to which to compare the performance of our plant functional type models. We used life forms related to basic plant physiology of all plant types in our study area, because we expected them to be easier to distinguish using imaging spectroscopy than more complex classifications (such as the Raunkier system), which are assumed to have a greater overlap in biochemical and structural characteristics. The life forms chosen are frequently used to define 'vegetation classes' in remote sensing and ecosystem modelling, as they are expected to be spectrally distinct due to presumed differences in biochemistry and structure. Likewise, we included growth forms of graminoids, which define the two most dominant grassland types in our study area, because of their ecological importance, as well as their assumed functional and spectral differences. We selected biochemical and structural traits (biomass, DM, N, NDF content), because they are known to influence the spectral signature of vegetation (Curran 1989). Moreover, these traits are known to be ecologically important (i.e. leaf economic traits), they are frequently used to define plant functional types, and among the most frequently measured traits world-wide (Kattge *et al.* 2011).

We calculated Spearman's correlation coefficients ( $R_s$ ) between the measured biochemical and structural vegetation traits (i.e. biomass, DM, N, NDF content) and the resultant plots × life forms, plots × growth forms and plots × functional types (i.e. plots × CSR strategy types, plots × indicator values) matrices. To illustrate the



correlation matrix, we used the *corrplot* package (Wei 2013) in R (version 3.1.2; R Core Team 2014).

#### IMAGING SPECTROSCOPY DATA

Imaging spectroscopy data were collected on 24 June 2010 between 09:00 and 12:00 h local time using the imaging spectrometer APEX operated on board a Dornier DO-228 aircraft. APEX is a dispersive pushbroom imager covering the wavelength range from 372 to 2540 nm with 312 spectral bands and a spectral sampling width ranging from 0.86 to 12.3 nm (Schaepman *et al.* 2015). We used 285 bands for analysis after removing noisy bands at the beginning and end of the spectrum. The ground sampling distance depends on flight altitude and ranged from 1.75 to 2.50 m (aircraft-ground distance between 3500 and 5230 m). All data were resampled to a regular pixel size of  $2 \times 2$  m using nearest-neighbour interpolation (Schläpfer & Richter 2002). Imaging spectroscopy data were geometrically and atmospherically corrected using the atmospheric radiative transfer model MODTRAN-5 as implemented in PARGE (Schläpfer & Richter 2002) and ATCOR-4 (Richter & Schläpfer 2002). Remaining geometric misregistration of the orthorectified data was evaluated and found to be <1 pixel in flat terrain and up to 2 pixels on steep slopes (Damm *et al.* 2012).

#### MODELLING

To model plant life/growth forms and plant functional types, we applied PLSR (Wold, Martens & Wold 1983) implemented in the *pls* package (Mevik, Wehrens & Liland 2013) in R (version 3.1.2; R Core Team 2014). We used the plots  $\times$  life forms, plots  $\times$  growth forms and plots  $\times$  functional types matrices of the research plot data as dependent and the plots  $\times$  spectral response matrices from imaging spectroscopy data as predictor variables. Since plots measured  $6 \times 6$  m and APEX pixel size was  $2 \times 2$  m, we calculated the mean reflectance per plot using a  $3 \times 3$  pixel window (see Schweiger *et al.* 2015). We applied leave-one-out cross-validation and limited the number of PLSR components by minimizing the cross-validated estimate of the root mean squared error of prediction (RMSEP). To evaluate model fit, we determined the correlation coefficient of multiple determination for the cross-validated predictions ( $R^2$ ) and Theil's uncertainty coefficient (Theil's  $U$ ), which has the advantage of taking deviations of the slope (from 1) and intercept (from 0) into account (Smith & Rose 1995). Values of Theil's  $U < 0.2$  indicate high and values from 0.2 to 0.4 indicate moderate predictive power. To make the performance of all models comparable, we calculated the RMSEP in percentages of the response range (RMSEP %) and the proportion of values predicted within <30% mean prediction error (<MPE %).

Finally, we assessed model consistency by comparing the predictions of the best PLSR models with the life/growth forms and functional types determined in the external validation data set. We extracted the predicted values of all pixels within each external validation plot and regressed the mean predicted values for each life/growth form and functional type against the life/growth forms and plant functional types determined from the relevés of the validation data set. To assess the accuracy of our models, we again calculated  $R^2$ , Theil's  $U$ , RMSEP (%) and the proportion of values predicted within <30% MPE (%). We used ENVI + IDL (version 4.7; Exelis Visual Information Solutions, Boulder, CO, USA) to extract reflectance values from, and apply the PLSR models to, the imaging spectroscopy data. All other analyses were conducted in R (version 3.1.2; R Core Team 2014; see Supporting Information).

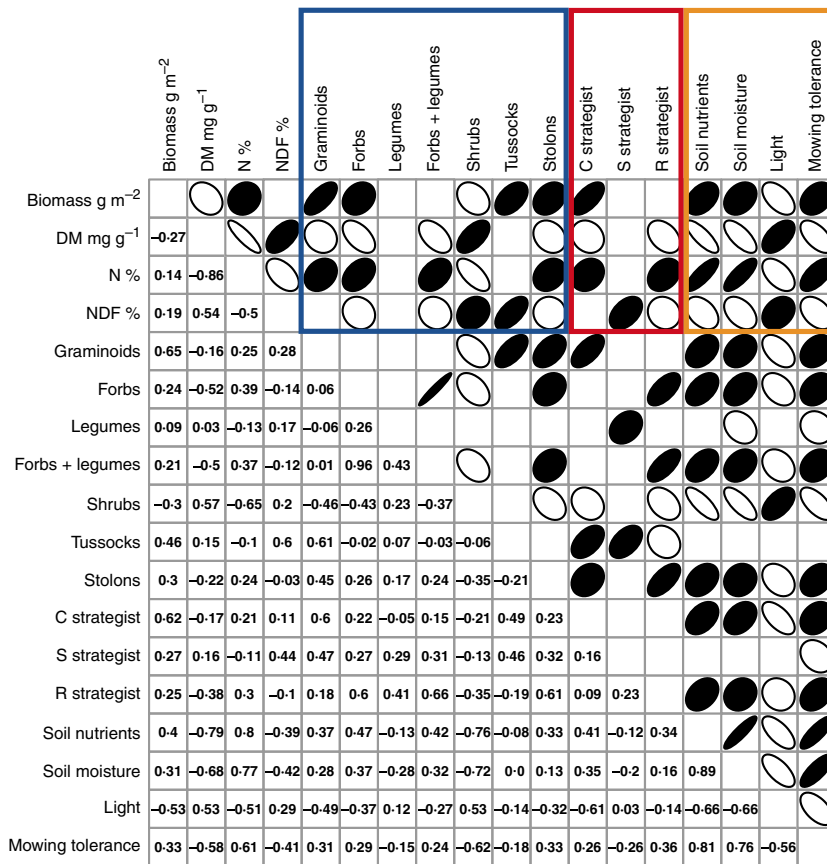
## Results

Correlation analyses between biochemical and structural vegetation community traits (biomass, DM, N and NDF content), plant life/growth forms and plant functional types (CSR strategy types and indicator values) revealed strong significant relationships for many of the pairs tested. Only legume cover was not significantly correlated with any of the biochemical and structural vegetation traits measured (Fig. 1). In addition, stolon cover showed comparatively low correlations, with the highest being  $R_S = 30\%$  for biomass (Fig. 1). This resulted in PLSR models being unable to detect the spectral characteristic of legumes and stolons, while the predictive power for all other life/growth forms was either high (Theil's  $U < 0.2$  for graminoids, forbs + legumes) or moderate (Theil's  $U \leq 0.31$  for forbs, shrubs, tussocks), explaining between 27% and 56% of total variation (Table 1; Fig. 2a,b). During external validation, however, model performance for all plant life/growth forms decreased considerably and model consistency was low (average change in  $R^2 = 72\%$ ). Only the models for forbs and shrubs retained moderate performance, explaining 18% and 19% of total variation, respectively (Table 1).

In contrast, PLSR models for all plant functional types had high predictive power (Theil's  $U \leq 0.2$ ), explaining between 28% and 62% of total variation (Table 1; Fig. 2c,d). An exception was the model for the indicator value for light availability, which had high predictive power, but only explained 16% of total variation, likely due to its small range of rather high values (Table 1). Model consistencies during external validation were considerably higher for plant functional types than for plant life/growth forms (average change of  $R^2 = 20\%$ ). Interestingly, even the indicator value for light availability was reasonably well predicted, explaining 24% of total variation in the external validation data.

We illustrate the spectral differences of vegetation communities with varying plant life/growth form cover and plant functional type abundances by plotting the means and standard deviations of spectra within the 1st and 10th deciles of each class. The spectra of plots within the 1st and 10th deciles of plant life/growth forms poorly predicted by PLSR did not show major differences, and the standard deviations around the mean of the deciles considerably overlapped across all wavelengths (Fig. 3c,f,g). In contrast, the spectra of plots within the 1st and 10th deciles of plant life/growth forms and plant functional types well predicted by PLSR, appeared generally more different, with the standard deviations around the mean of the deciles overlapping less. The regions of the spectrum showing the largest differences varied, with graminoids and CSR strategy types being noticeably different in the visible part of the spectrum (*c.* 370–700 nm; Fig. 3a, h–j), forbs, shrubs, C strategists and indicator plants being different in the near-infrared (*c.* 700–1400 nm; Fig. 3b,e,h,k–n), and S strategists and soil moisture indicators showing additional differences in the shortwave-infrared (*c.* 1400–3000 nm; Fig. 3i,l).

Our approach for predicting plant functional types using imaging spectroscopy is summarized in a conceptual



**Fig. 1.** Correlation matrix between biomass (Biomass g m<sup>-2</sup>), dry matter (DM mg g<sup>-1</sup>), nitrogen (N %) and neutral detergent fibre (NDF %) content, plant life forms (graminoids, forbs, legumes, forbs + legumes combined, shrubs; cover %; blue square), growth forms of graminoids (tussocks and stolons; cover %; blue square) and seven plant functional types of two categories: CSR strategy types [competitive (C), stress-tolerant (S), ruderal (R) strategist; scores; red square] and indicator values (soil nutrients, soil moisture, light, mowing tolerance; orange square) measured at the vegetation community level. The upper triangle shows significant correlations ( $P < 0.05$ ) only, with the direction (black = positive, white = negative) and strength (thick = weak, thin = strong) indicated by the ellipses. The lower triangle shows all values for Spearman's correlation coefficient ( $R_s$ ).

framework (Fig. 4). The spectral response of the vegetation community (red ellipse, plots  $\times$  spectral response) and plant functional type classifications (blue ellipse, plots  $\times$  PF types) are determined by covarying biochemical and structural vegetation traits (plots  $\times$  community-level traits). Plant inventories (blue ellipse, plots  $\times$  species) can be used to determine the abundance of plant functional types at the vegetation community level (blue ellipse, plots  $\times$  PF types). As long as plant functional types and plant functional traits are tightly correlated, as was the case in our study, this relationship links the functional and spectral signatures of the vegetation community (orange ellipse) and allows predicting plant functional types at the vegetation community scale.

## Discussion

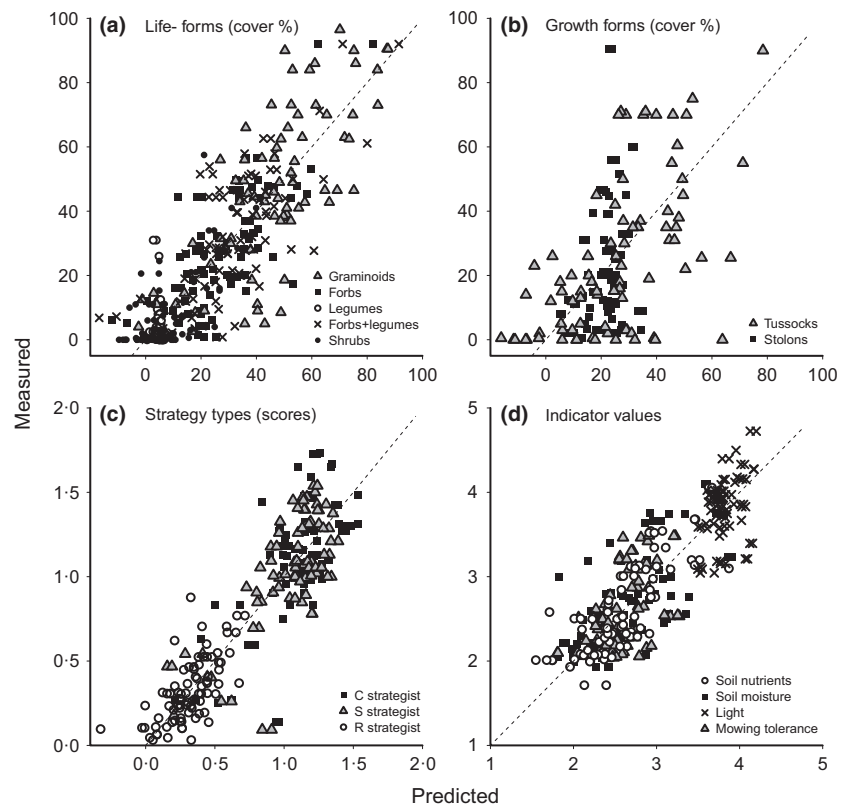
Our results showed that imaging spectroscopy enables modelling and predicting plant functional types at the vegetation community scale with high accuracy and greater consistency than plant life/growth forms. The ability of imaging spectroscopy to predict plant functional types can be explained by their strong correlations with biochemical and structural vegetation traits, as well as the differences among plant functional types regarding biochemistry and structure (Fig. 1). In summary, we argue that detecting plant functional types using imaging spectroscopy can offer advantages over the more common use of plant life/growth forms, because plant functional type classifications are based upon causal relationships to

biochemical and structural vegetation traits. These correlations are central for spectroscopic applications, since the reflectance properties measured likewise depend on biochemical and structural vegetation characteristics. Strong causal relationships between plant functional types and functional traits form the backbone of plant functional type theory and have been confirmed for a variety of ecosystems world-wide (Cornelissen *et al.* 2003; Wright *et al.* 2004; Reich, Wright & Lusk 2007). We thus assume the relationship between the vegetation communities' functional and spectral response to hold at global scale (Lausch *et al.* 2016).

Generally, plants trade off their investment in photosynthesis against life span and structural components of leaves (Reich, Walters & Ellsworth 1997), trade-offs that are accompanied by different strategies of reproductive development and growth (Cerabolini *et al.* 2010). Plants that invest in fast growth and early and extensive flowering (R strategist) can be expected to have high leaf N content, as the main CO<sub>2</sub>-fixing enzyme RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase) accounts for 30–60% of the total N content in plants (Elvidge 1990). However, these plants usually have fewer resources for structural components of leaves and stems, and thus can be expected to have lower DM and NDF content. In contrast, plants able to persist in low-resource environments (S strategists) invest more in structural tissue components, and thus usually have high DM and/or NDF content, but low N content. C strategists are positioned between these two extremes; apart from considerable investments in

**Table 1.** Results of partial least squares regression (PLSR) models predicting plant life and growth forms and seven plant functional types of two categories (CSR strategy types, indicator values) at the vegetation community level, and external model validation. Model fit and accuracy are described by the correlation coefficient of the cross-validated predictions ( $R^2$ ), Theil's uncertainty coefficient (Theil's  $U$ ), root mean squared error of prediction (RMSEP, %) and the per cent of predicted values below a mean prediction error of 30% (<MPE, %). The number of PLSR components (ncomps) and the value ranges, described by the minimum (min), maximum (max) and mean  $\pm$  standard deviation (SD), are indicated

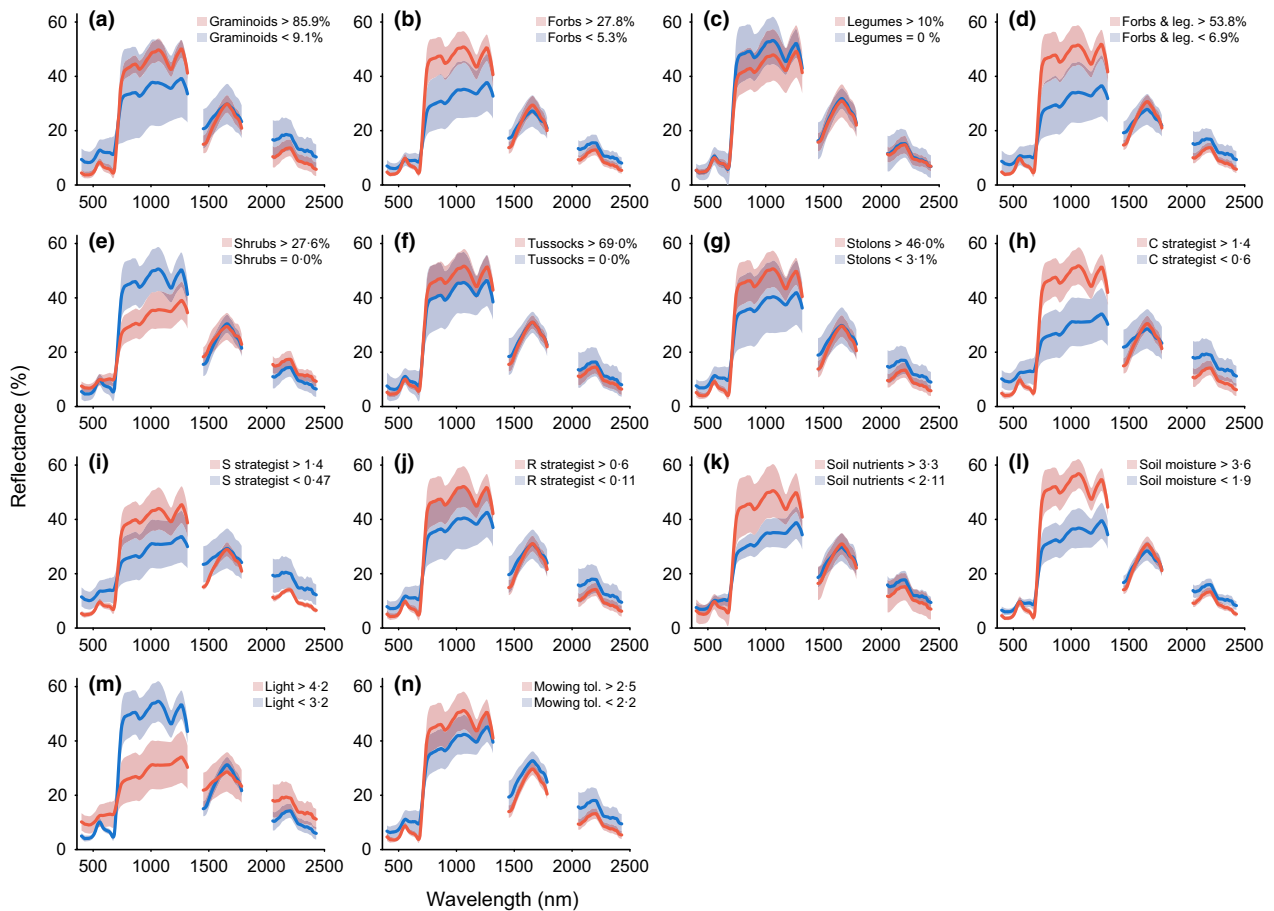
	PLSR model					Value range		External validation			
	$R^2$	Theil's $U$	RMSEP (%)	<MPE (%)	ncomps	Min-Max	Mean $\pm$ SD	$R^2$	Theil's $U$	RMSEP (%)	<MPE (%)
Life form (cover %)											
Graminoids	0.56	0.17	17.3	58.5	12	2.6–96.5	46.3 $\pm$ 26.1	–0.03	0.27	28.8	38.9
Forbs	0.52	0.20	13.0	45.1	11	0.7–92.0	27.4 $\pm$ 18.7	0.18	0.24	18.2	63.9
Legumes	–0.06	0.50	6.2	23.2	1	0.0–31.0	4.6 $\pm$ 6.1	–0.02	0.70	21.7	19.4
Forbs + Legumes	0.50	0.19	14.1	51.2	10	0.8–92.0	32.0 $\pm$ 20.2	0.08	0.28	29.5	50.0
Shrubs	0.47	0.31	8.8	23.2	12	0.0–57.5	8.7 $\pm$ 12.2	0.19	0.41	10.3	30.6
Growth form (cover %)											
Tussocks	0.27	0.30	20.2	31.7	12	0.0–90.0	25.1 $\pm$ 23.9	–0.03	0.47	24.8	16.7
Stolons	0.09	0.36	18.3	28.1	2	0.5–90.5	21.2 $\pm$ 19.3	0.10	0.32	19.2	27.8
Strategy type (scores)											
C strategist	0.45	0.12	0.27	82.9	5	0.14–1.73	1.09 $\pm$ 0.37	0.37	0.11	0.26	83.3
S strategist	0.52	0.11	0.24	84.1	7	0.09–1.54	1.03 $\pm$ 0.35	0.28	0.11	0.25	86.1
R strategist	0.39	0.20	0.15	54.9	10	0.03–0.88	0.33 $\pm$ 0.19	0.36	0.25	0.23	50.0
Indicator value											
Soil nutrients	0.62	0.06	0.34	98.8	7	1.71–4.06	2.60 $\pm$ 0.55	0.58	0.08	0.44	94.4
Soil moisture	0.40	0.08	0.43	95.1	10	1.93–4.10	2.68 $\pm$ 0.56	0.38	0.08	0.44	91.7
Light	0.16	0.04	0.34	100	1	3.04–4.73	3.82 $\pm$ 0.37	0.24	0.03	0.21	100
Mowing tolerance	0.28	0.08	0.40	98.8	5	2.03–3.49	2.59 $\pm$ 0.47	0.30	0.09	0.48	88.9



**Fig. 2.** PLSR models predicting (a) the % cover of plant life forms (graminoids, forbs, legumes, forbs + legumes combined, shrubs), (b) the % cover of growth forms of graminoids (tussocks, stolons), (c) CSR strategy type scores [competitive (C), stress-tolerant (S), ruderal (R) strategist] and (d) indicator values (soil nutrients, soil moisture, light, mowing tolerance) in our 50 research plots. The dotted line represents the 1 : 1 line; for model fit and accuracy (see Table 1).

photosynthesis, they must also invest in durable tissues, allowing them to overtop their neighbours, resulting in high biomass, high N content and more structural components (higher

DM and/or NDF content) than R strategists (Cerabolini *et al.* 2010). These relationships have been found in a variety of ecosystems (e.g. Hodgson *et al.* 1999; Cerabolini *et al.* 2010;



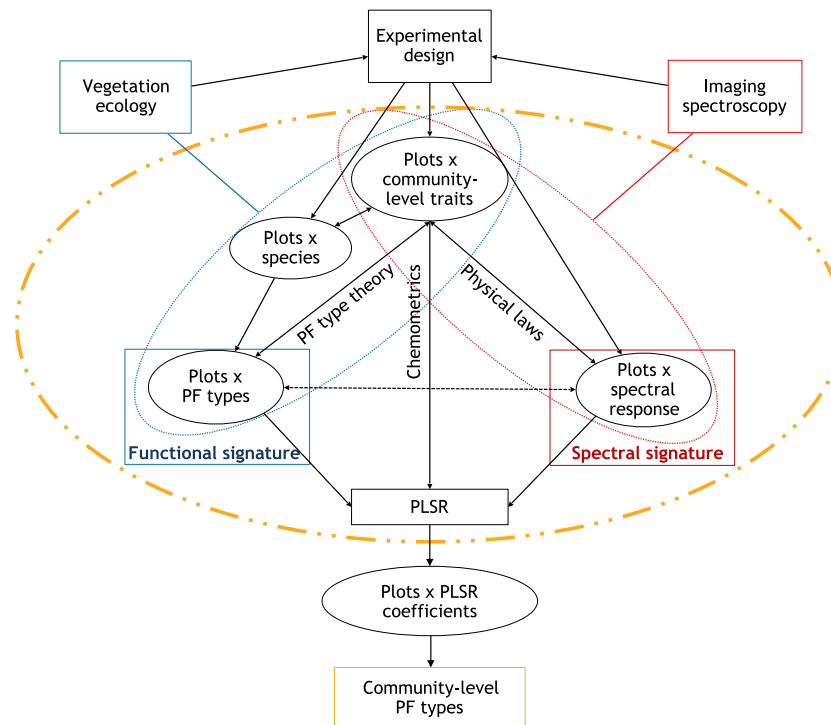
**Fig. 3.** Mean and standard deviation of airborne imaging spectroscopy spectra from vegetation communities within the 1st (red) and 10th deciles (blue) of life/growth form cover (a–g), competitor scores (h–j) and indicator values (k–n). The decile class limits are indicated.

Negreiros *et al.* 2014) and were confirmed by our study (Fig. 1). Likewise, the concept of indicator species is based on relationships between soil biogeochemistry and biochemical and structural vegetation traits (Diekmann 2003). We were able to confirm strong correlations between biochemical and structural vegetation traits and Ellenberg's indicator values (Ellenberg *et al.* 1991) (Fig. 1), which allowed us to model and predict them with high accuracy and consistency (Fig. 2; Table 1).

In contrast, our results point out that the relationships between plant life/growth forms and biochemical and structural traits can be more variable. Generally, this occurs when species having different functional characteristics are causing high variability of leaf traits – such as DM, N, fibre content, and associated leaf anatomy, photosynthetic capacity and longevity – within classes and broad overlaps between them (Kattge *et al.* 2011). This can lead to little distinctiveness between the leaf optical properties of vegetation classes, which complicates their spectral detectability. For example in our case, the two tussock grasses *Deschampsia cespitosa* (L.) P. Beauv. and *Nardus stricta* L. differed substantially in functional characteristics. *Deschampsia* occurs on nutrient-rich soils where it invests in rapid, tall growth, forming large, green tussocks with relatively low fibre content. In contrast, *Nardus* sustains itself on steep slopes having shallow,

nutrient-poor, parched soils, where it forms small, bristly, fibre-rich tussocks. Consequently, these two tussock grass species are completely different in biochemical and structural traits, contributing to high trait variability within the growth form 'tussock grasses', reducing their discrimination based on leaf optical properties and hence complicates their detectability with imaging spectroscopy. This said, *Deschampsia* and *Nardus* are separable by plant functional type as reflected by both CSR strategy type and indicator classification (*Deschampsia*: C strategist, indicator for nutrient- and moisture-rich soils; *Nardus*: S strategist, indicator for nutrient- and moisture-poor soils), which are by definition tightly coupled to biochemical and structural plant traits and thus separable using spectral signatures. Other graminoids, as well as forbs and shrubs, likewise occurred in areas differing in topography, soil and microclimatic conditions, spanning a large gradient of environmental conditions in our study area. Thus, although several plant life/growth forms were fairly well correlated with biochemical and structural vegetation traits in our input data (Fig. 1), trait variability within groups in our study system was likely too high to allow models to be consistent (Table 1). We are aware that tighter relationships between plant life/growth forms and biochemical and structural traits, including ones not explicitly tested in this study, may exist in other environments. While the





**Fig. 4.** Conceptual framework using the theory and methodology of vegetation ecology (blue ellipse) and imaging spectroscopy (red ellipse) to link the functional to the spectral signature of the vegetation community. According to plant functional (PF) type theory, the vegetation community (plots  $\times$  species) integrates environmental conditions and allocates resources towards the expression of covarying biochemical and structural traits, measurable at the community scale (plots  $\times$  community-level traits) and causally linked to plant functional types (plots  $\times$  PF types). The reflectance of vegetation measured using imaging spectroscopy (plots  $\times$  spectral response) is determined by reflection, transmission and absorption of light (physical laws), which again depend on biochemical and structural traits (plots  $\times$  community-level traits). In this study (orange ellipse), we connect plant functional types and the spectral response via their link to biochemical and structural vegetation traits and suggest partial least squares regression (PLSR) model coefficients, commonly used in chemometrics, to predict plant functional types at the vegetation community level.

relationship between vegetation traits and plant life/growth forms might hold true for ecosystems that are generally species-poor or are rather uniform with respect to soil and microclimatic conditions, these relationships can be expected to weaken in areas where soil conditions, microclimate and topography vary substantially. This in turn reduces the ability of imaging spectroscopy to detect life/growth forms, which could lead to models becoming inconsistent, as was the case in our study area. Thus, we argue that the spectral detectability of plant life/growth forms as well as their usefulness for ecosystem monitoring and environmental modelling will depend on the ecosystem system and vegetation community under study.

According to our results, PLSR coefficients can serve as proxies for the combined biochemical and structural characteristics of plant functional types, linking a vegetation community's functional and spectral responses. Although model coefficients from empirical methods, such as PLSR, will usually vary from site to site and are thus not directly transferrable, they can be applied to different study systems, as long as the variables included in the model cover the entire expected variability (Martens 2001). As predictions of negative values, for example for cover per cent (Fig. 2a,b), are clearly nonsensical, the implementation of a PLSR algorithm that constrains predictions to positive values would be a valuable research contribution.

Comparing the spectra of plots having high and low life/growth form cover or plant functional type abundances indicates when pattern detection techniques, such as PLSR, can be expected to differentiate spectral signals (Fig. 3). Similar spectral responses within plant life/growth forms or plant functional type classes can point not only towards little spectral distinctiveness, but also towards a narrow range of values in the data, both of which complicate spectral separability. In addition, more variable spectral regions can point to high trait variability within classes, for example regarding pigment composition (in the visible part of the spectrum), structural composition or water content (in the near- and shortwave-infrared; e.g. Curran 1989). Quantitative assessments of more variable vs. more conserved spectral regions and their relationships to leaf optical characteristics and vegetation community traits will be an important task for future research, enabling general rules for the optical differentiation of plant functional types, and plant life/growth forms to be established.

As imaging spectroscopy data become more widely available and ground reference data for plant functional types and plant life/growth forms can be derived from botanical relevés, it will become possible to test under which conditions detecting plant functional types provides advantages over detecting plant life/growth forms. Initiatives to join plant functional trait, plant functional type and spectral data bases, such as TRY (Kattge *et al.* 2011), EcoSIS (University of Wisconsin-



Madison 2016) and Specchio (Hueni *et al.* 2009), will amplify the opportunities to test our framework in different regions. Additionally, the launch of new remote sensing instruments, in particular the spaceborne imaging spectrometers EnMAP (planned in 2018; DLR 2015) and HypSIRI (planned after 2022; NASA 2012), will enable comparative studies investigating the relationships between spectral response curves of vegetation communities, functional vegetation characteristics and ecosystem processes on a global scale.

Summarized, our results demonstrated that imaging spectroscopy data can be successfully used to model and predict plant functional types, as PLSR coefficients serve as proxies for the combined characteristics of biochemical and structural vegetation community traits. This link between a vegetation's functional and spectral signatures can facilitate large-scale ecosystem monitoring as both data types share advantageous characteristics: (i) they are generalizable and thus can be used across large spatial scales; (ii) they are integrative and hence allow the detection of not only single factors, but also processes; (iii) both are directly linked to plant functional traits ensuring their interpretability; and (iv) they can be used on an ecologically relevant and practicable level: the vegetation community scale.

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## Data accessibility

R script and data sets can be found in the Supporting Information.

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## Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

**Appendix S1.** R code to (i) test correlations between functional traits, plant life/growth forms and plant functional types, (ii) illustrate the results of the correlation analysis and (iii) run partial least squares regression (PLSR) to model and predict plant life/growth forms and plant functional types using imaging spectroscopy data (example: graminoids).

**Appendix S2.** Vegetation community trait values for biomass ( $\text{g m}^{-2}$ , Biomass\_g  $\text{m}^2$ ), dry matter ( $\text{mg g}^{-1}$ , DMC\_mg\_g), nitrogen (% N\_perc) and neutral detergent fibre content (% NDF\_perc) and per cent (%) cover data for plant life/growth forms (graminoids, forbs, legumes, forbs and legumes combined, shrubs, tussocks, stolons), CSR strategy type scores [competitive (C), stress-tolerant (S), ruderal (R) strategist] and indicator values (soil nutrients, soil moisture, light, mowing tolerance) measured in our research plots.

**Appendix S3.** Per cent (%) cover data for the plant life/growth forms (graminoids, forbs, legumes, forbs and legumes combined, shrubs, tussocks, stolons), CSR strategy type scores [competitive (C), stress-tolerant (S), ruderal (R) strategist] and indicator values (soil nutrients, soil moisture, light, mowing tolerance) measured in our research plots.

**Appendix S4.** Mean reflectance spectra from our research plots acquired by the imaging spectrometer APEX.